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# AN ATTEMPTED ANALYSIS OF PARASITISM

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(WITH SIX FIGURES)

According to a recently published estimate made by the author, about half of the total number of seed plants use complex food material derived from other organisms by mycorhizal or parasitic arrangements. So far as our observations go, dependent species, which are advantaged by contact or association with other species, undergo direct somatic modifications, consisting chiefly of atrophies or reductions of the shoot and root system; and in plants of fixed parasitic habit, these reductions may be such as to include the total disappearance of the roots and to bring the shoot down to simple, unbranched, chlorophylless stems, upon which the leaves are represented by colorless bracts. The fruits and seeds may show various specializations.

During the course of an extensive investigation of the conditions under which two species may enter into the relation of host and parasite, regenerated cuttings of a large number of species were attached to the stems of desert succulents and xerophytes. In some cases the attached plants formed roots; and in others the epidermal cells performed the function of absorption.

The ruling factor was in all cases the osmotic ratio between the sap of the two plants; one plant may not become parasitic upon another except by the aid of a superior osmotic pressure which withdraws solutions from the tissues of the enforced host. Many causes, however, may operate to prevent a potential parasite from becoming actual, such as the formation of wound-cork, excretions, periodic alterations in turgidity, etc. The physiological alterations consequent upon the arrangement of two plants in a xeno-parasitic relation are of a saltatory or mutative character, yet no evidence is at hand as to the manner in which such alterations become fixed and transmissible. A perfectly graded series of parasites may be selected which exemplify all stages of dependency, atrophies or reductions, and adjustive arrangements; but nothing may be assumed as to the manner in which progress has been made from one stage to another. It seems fair to conclude, however, that the evolutionary movement is generally toward increased dependency of the parasite, accompanied by accentuated and more complete atrophies. The view that such a movement may sometimes ultimately lead to extinction, although by a long and indirect way, seems also justifiable by inference, although such an end must not be assumed for all groups of parasites.

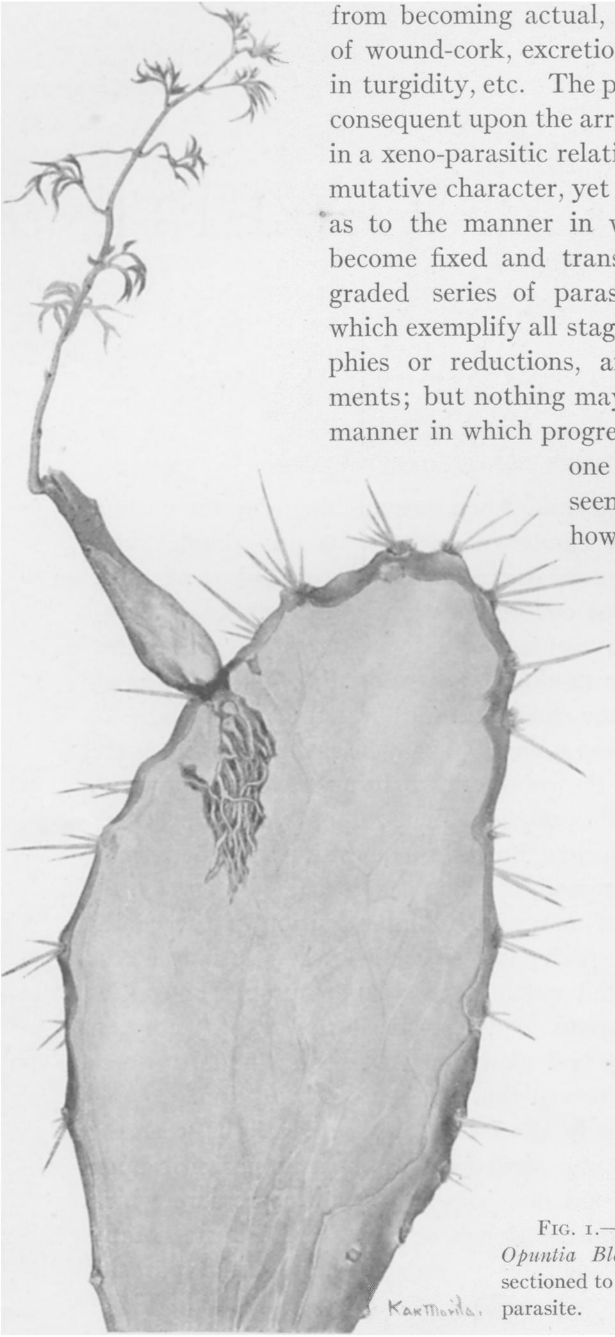

FIG. 1.—*Cissus laciniata* parasitic on *Opuntia Blakeana;* the host has been sectioned to expose the roots of the xeno-parasite.

In the experiments carried on at the Desert Laboratory from 1908 to 1911, the desert grape (*Cissus laciniata*) of Mexico, the expressed juice of which shows a pressure of over 11 atmospheres, was found to maintain itself on the flattened joints of *Opuntia Blakeana* at about 9 atmospheres; not so successfully on *Echinocactus Wislizeni*, the drinkable juice of which has a concentration equivalent to about 6 atmospheres; while it soon perished when attached to stems of the great tree cactus (*Carnegiea gigantea*) at less than 7 atmospheres (fig. 1). The last named plant exudes an acrid fluid from fresh wounds, which are quickly closed by the formation of heavy, corky layers. *Opuntia versicolor*, a species with cylindrical stems showing a pressure of 12 atmospheres, was able to draw supplies for extended periods from *Carnegiea* and the other hosts mentioned. Plantlets of *Agave* were equally efficient, although this xeno-parasite formed such a great number of roots as to destroy the tissues of the host plant. *Cissus* also formed roots which penetrated the host, while the absorptive contact of *Opuntia* (flat-stemmed) was by the epidermal cells of the stems in every case examined.

The briefest inspection of the results of the analysis of plants used in these experiments, shows that the direct proportion of mineral salts in the sap and the acid contents of the sap have no direct bearing on possible parasitism among the higher plants.[1] The relation of seasonal cycles, capacity for development of absorptive elements *de novo*, and an accommodative adjustment of the osmotic pressure of the cell sap are to be mentioned as factors in the making of nutritive couples. The greater number of the parasitic arrangements made are to be included with the root parasites.

A few additional experiments were set up to test certain points after the completion of the manuscript printed in 1910. The results of these and of the continuation of older preparations seem to warrant the presentation of this additional note on the subject.

*May 11, 1910.*—A number of beans of a mixture of species native to the deserts of southern Arizona were attached to joints of prickly pear, with the radicles thrust into cavities in the soft tissue. The bean was held in place by a setting of plaster of Paris, and a moist strip of cloth was brought from a vessel of water to furnish moisture until the plants should become established in their new relations.

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[1] See MacDougal and Cannon, The conditions of parasitism in plants. Publ. No. 129, Carnegie Inst. of Wash. 1910.

*May 13.*—A large number of new insertions of the "rusty" bean in joints of *Opuntia* and bodies of *Carnegiea* and *Echinocactus* were made on this day. Some of the original preparations were showing notable growth.

*May 14.*—Some of the plants first arranged had thrust the tips of the plumules beyond the cotyledons, but had not yet straightened the hypocotyl. One bean with wilted plumule was taken out of the *Opuntia*. The main root had grown but little. A secondary branch from near its base had come out and extended down into the cavity, alongside the main root, showing as great a length.

*May 22.*—Twelve seedlings on *Opuntia* had survived, of which one had developed the plumule to an extent that the leaves were unfolding from between the cotyledons. Six seedlings on *Echinocactus* had survived, and were showing some slight development. Three seedlings out of 9 insertions on *Carnegiea* had survived and had made a slight development. The cotyledonary curvature was still markedly present.

*May 31.*—Temperatures of 111° and 112° F. out of doors, and all parasites were flagging, apparently dying. All soon perished.

About a dozen germinated beans of the form known as "small Papago white" were inserted in joint of "Mission Pear" (*Opuntia* sp.), near the laboratory at Carmel, California, on June 23, without any protection except a cloth shade. These, with the exception of two, dried out, although small secondary roots were formed by June 27. All were replaced and a small vial was arranged with a strip of cloth to give shade and moisture. About 8 similar preparations were arranged on *Oenothera biennis* and *O.H.206.* On July 1, only one of this lot had become dry, the fogs of the preceding days having been an obvious advantage.

*July 14.*—Seven Papago white beans on Mission Pear thriving, of which three had well developed leaves of the first simple pair, and one showed a second pair. The others still retained the plumule partly between the cotyledons.

*August 2.*—All beans were dead or nearly so. All of the development in these plants was undoubtedly carried on at the expense of material in the cotyledons; and the roots soon perished after being immersed in the mucilaginous tissues of *Opuntia* or the stems of *Oenothera.* The high humidity of the fogs and low temperatures ranging between 45° and 65° F. also made for the endurance of the seedlings. These tests are chiefly interesting in contrast with the cultures of PEIRCE, in which plants of *Pisum sativum* were grown on stems of *Vicia Faba* to maturity. The advantage of the aeration of the roots in the central cavities of the stems of the host and also of one legume parasitic upon another, doubtless accounts in large measure for the success of these cultures.[2]

The completion of the original manuscript on this subject left several preparations in good condition, which were two years old. Among these were *Opuntia Blakeana, O. versicolor, O. arbuscula,* and *O. leptocaulis* on *Carnegiea; O. leptocaulis* on *O. discate;* also one *Agave americana* on *Carnegiea.* Some of these parasites remained alive throughout a part or all the year, it being noted that those shielded from direct illumination by the body of the host survived longest. March 1911 found arrangements of *Opuntia versicolor, O. Blakeana,* and *Agave* on *Carnegiea.*

All these preparations were made with plants as xeno-parasites which were characterized by a water balance of some amount and by an osmotic pressure of the sap of 9–12 atmospheres. Furthermore, the survivors were held in place by a mass of plaster of Paris molded about the bases of the stems which held the roots closely appressed against the corky tissues of the host.

This state of affairs may be seen to furnish a fair approximation of the physical conditions under which an *Opuntia* was found with the roots in a small cavity in the trunk of a *Parkinsonia,* and of the same species in a cavity in the summit of a trunk of *Carnegiea.*[3] A further illustration is offered by a case photographed and reported

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[2] PEIRCE, G. J., Artificial parasitism, etc. BOT. GAZ. **38**:214. 1904.

[3] See Publ. No. 129, Carnegie Inst. of Wash. 1910.

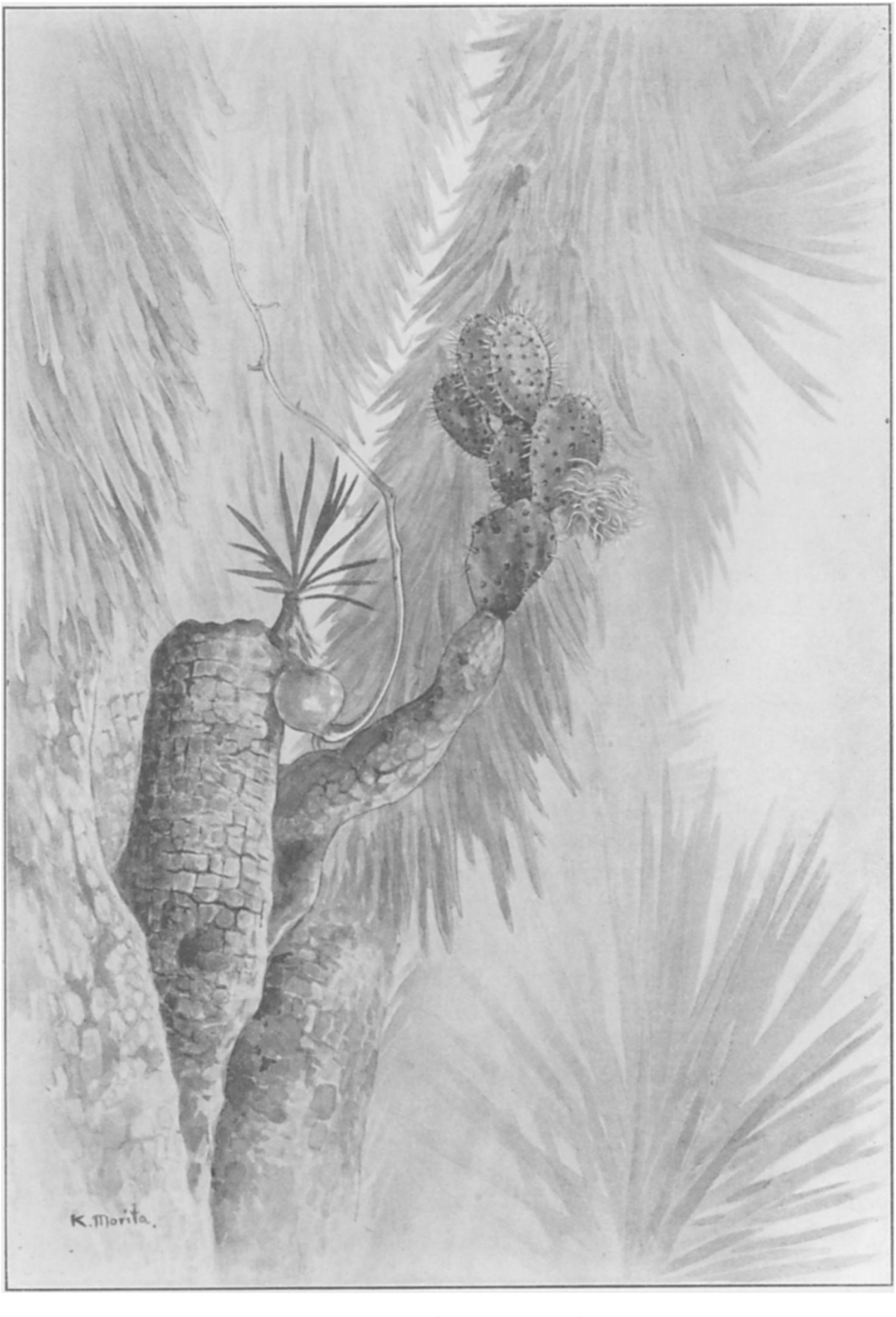

FIG. 2.—*Cissus laciniata* and *Opuntia* growing from sinus in stem of *Yucca*, near Tehaucan, Mex.; an epiphytic bromeliad is attached to one of the terminal joints of the *Opuntia*.

by Dr. W. A. Cannon, in which a flat-jointed *Opuntia* was found established in a cavity in the trunk of an *Acacia Greggii.* One or more species of *Opuntia* native to the Tehuacan region find a foothold in the crevices of tile roofs, and stone and adobe walls, in a very noticeable manner; and it was in this vicinity that one of these plants and a native grape were found rooted in the sinus of a forked tree *Yucca* (fig. 2).

The conditions of such association seem favorable for the slow extraction of solutions from the host plant through non-living tissues without the actual contact of the living cells, an approximation to the initial conditions of parasitism. It is obvious that the crowded root systems of a wide physiological variety of plants in the soil furnish numberless duplications of these conditions, and it seems entirely reasonable to suppose that such contiguity of absorbent and succulent roots may acccount, in part, for the greater number of root parasites.

It is to be noted that among the higher plants the part played by destructive secretions is at a minimum. The activity or absence of such substances in seed parasites has been variously described. In no instance, however, are there such abundant and disintegrating effects as may be seen resulting from bacterial and fungal parasites of plants and animals.

The parasitic arrangements described above, in which the host furnishes lodgment and a slowly yielded supply of solution, are characterized by a slow growth of the parasite, in which the amount of development is limited, the members being reduced. The *Opuntia* parasitic on *Parkinsonia,* which was described in *Publication No. 129,* Carnegie Inst. of Washington, 1910 (see pl. 10), was taken from the host early in 1910 and set in the adobe soil of the terraces in the courtyard of the Desert Laboratory. In the course of the growing season of that year, it made three new joints, each of which was three or four times the bulk of those previously formed, the total growth in the previous 7 or 8 years. Furthermore, in this autophytic growth it developed characters which demonstrated that it properly belonged to *Opuntia Toumeyi* instead of *O. Blakeana,* with which it was first identified, because of its small joints and atrophied spines (fig. 5).

The *Opuntia versicolor* which had been fastened in a cavity in the side of a tall *Carnegiea* early in 1909, lost three of its four short branches and the terminal section of the stem during the dry foresummer of 1910. Activity in the rainy season in the midsummer following resulted, not in the formation of additional sections or members, but in the increase in thickness of the stem and roots; the latter were thin and fibrous when the preparation was made, January 23, 1909. After two years of parasitic existence, the visible portions of the root system were much enlarged, after a manner sometimes exhibited by autophytic individuals of the same species (figs. 3 and 4).

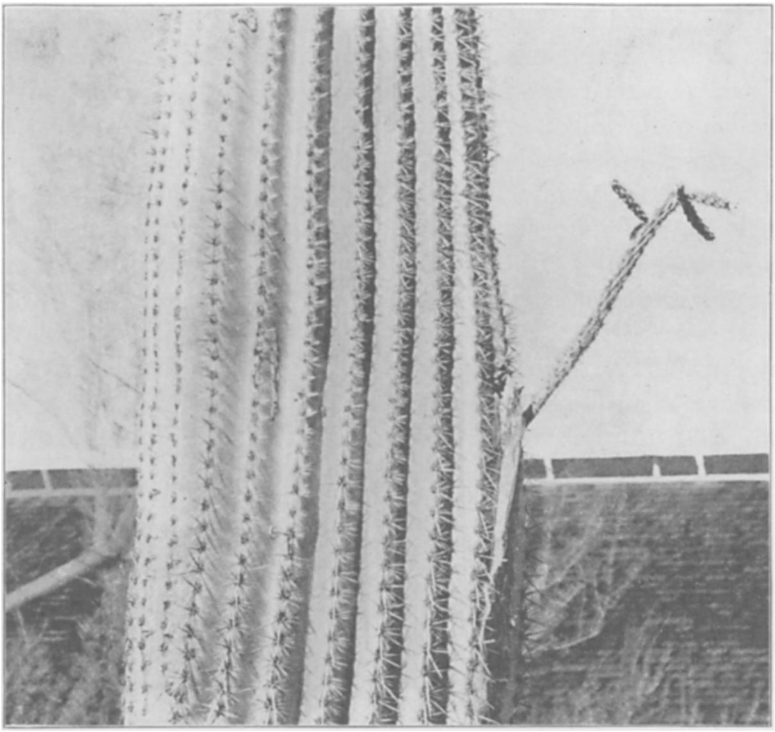

FIG. 3.—*Opuntia versicolor* parasitic on *Carnegiea gigantea*, March 1910

An *Opuntia Blakeana* set in a cavity of *Carnegiea*, where it was held by plaster, early in 1909, likewise formed no additional members during the following two years. Some thickening of the cylindrical basal segment, however, was noticeable.

The work described in this and previous papers has been successful in the demonstration of certain physical conditions which make parasitism possible, and has led to the suggestion of physiological activities which limit or facilitate the adhesion of two seed plants in a dependent nutritive combination. Wider observations would doubtless increase the known parasitic combinations, while it may be safely assumed that present conditions are as favorable for their making as at any time in the history of the plant world. New parasites may be expected to be brought to our attention from time to time.

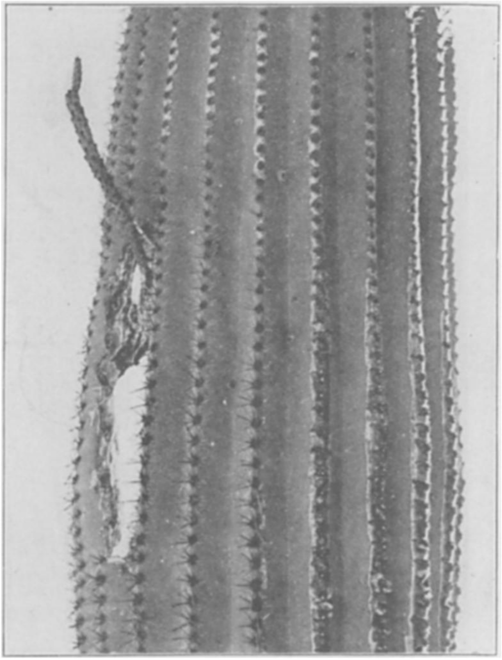

FIG. 4.—Same plant as in fig. 3, March 1911, with enlarged roots and stem, and with but one surviving branch.

The assumption of a mutualistic or dependent rôle, in fact any departure from a purely autophytic condition by a green plant, is inevitably followed by reductions or atrophies. Such combinations are displayed by a number of seed plants, not far short of half the existing species. It is of interest to note that the parasitical consequences have not yet been seen in green plants furnished with food material including organic compounds. The total reaction is complex, and the exciting causes are probably not simple. Whatever they may be, they are furnished only by the living or decaying bodies of other organisms. The part played by the pathological effects and physiologic reactions of parasites in the evolutionary development of plants has never been adequately portrayed, even in a speculative manner.

The vigor of growth, widely varied capacity for reproduction, range of endurance to unfavorable conditions, and accommodational adjustment displayed by parasitic fungi and bacteria in general seem to place the greater majority of these forms in a

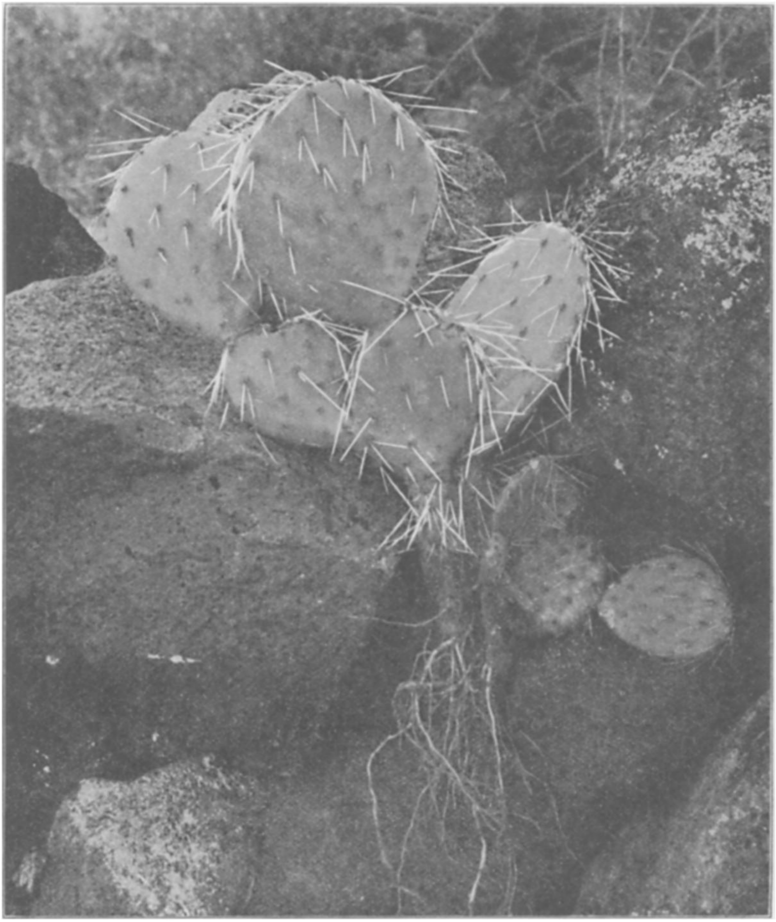

FIG. 5.—*Opuntia Toumeyi;* this plant was found growing in a cavity of the trunk of a small tree of *Parkinsonia microphylla* in 1906, and the small joints formed during its parasitism are to be seen near the base and to the right; the larger joints were developed after the plant began an autophytic existence rooted in the soil; photographed February 1911.

position where the only obvious way to extinction would be by the destruction of their hosts, resulting from their own effectiveness. Nothing known of the life history of any of these forms suggests a possible abandonment of the parasitic habit and of an advancing morphological development. So far as the higher plants are concerned, the only consideration hitherto given to parasitic forms has been to view them as passing down an inclined plane of atrophies, which would ultimately lead to their extinction, without reference to the abundance of development of the host forms. No hint has yet been obtained as to the possibility of a retracement, by which a dependent might once more regain its standing as an autophyte.

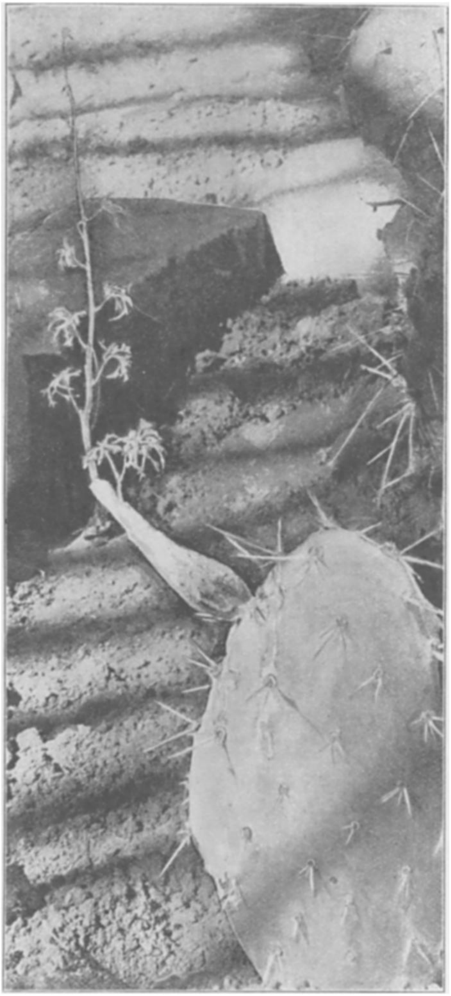

FIG. 6.—*Cissus laciniata* parasitic on *Opuntia Blakeana* (see fig. 2).

Regressive action of this character would naturally be discernible only in a series of material extending over long periods of time, such as that obtained by the paleontologist. It is interesting to note that this subject is one to which some serious attention has been given, and Dr. J. M. CLARKE[4] has recently summarized the information with regard to the case of the limpet and the crinoid of earlier times and the gastropods and sea urchins of the present. It is made clear by CLARKE that the limpets of the early Silurian were largely parasitic on the crinoids, a habit that persisted for millions of years, until the closing stages of the Paleozoic, when evidences of it were lost, and no traces of parasitism of snails on the few crinoids of the present are known. Other gastropods of the limpet structure are now parasitic on the starfish and sea urchins, close relatives of the crinoids. The earlier limpets were not carried beyond the stage of possible regression in their parasitism, but the modern parasitic gastropods are "often so modified by their degeneracy that their nature is hardly recognizable, and this parasitism is fixed and beyond repair." Two separate cases of adaptational adjustments seem involved, and the parasitism of the modern gastropods is taken to be wholly independent of the earlier assumption and abandonment of the habit. The suggestion lies near, however, that a family which has thus furnished two separate series of parasites is one which by morphological characters or physiological tendencies is liable to assume dependent relations with other organisms as hosts. Parasitism among the higher plants of the present time is confined to ten families, one of which has been added recently to the list by the work of Dr. W. A. CANNON. It may be safely assumed that in some of these, the Orobanchaceae, for example, the habit is far beyond retraction.

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[4] The significance of certain early parasitic conditions. Science **33**:291. 1911.

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